

Tree size, microhabitat, and hydraulic traits (interactively) shape drought response in a temperate broadleaf forest

Ian McGregor, Ryan Helcoski, Norbert Kunert, Alan Tepley, Valentine Herrmann, Joseph Zailaa, Atticus Stovall, Neil Pederson, Lauren Sack, Krista Anderson-Teixeira

Abstract

Predicting forest responses to drought is an increasingly critical task under climate change effects. Part of the problem is due the lack of a set definition of drought in recent studies, while often the effects of biophysical and hydraulic traits are interpreted separately. In this study, we analyze the interaction between these two trait groups using forest census data from a 25.6-ha ForestGEO plot in Virginia (USA). Drought periods were defined by both Palmer Drought Severity Indices (PDSI) and their identification from tree-ring records for 12 species representing 97% of woody productivity. Each drought scenario (1964-66, 1977, 1999), along with the overall trend, was then tested against leaf hydraulic trait measurements and microhabitat biophysical data. Individual-level growth responses to three droughts were stronger among taller trees in dominant canopy positions, those in wetter microsites, and for more drought-sensitive species as assessed by leaf traits (turgor loss at less negative leaf water potential, greater shrinkage with leaf dehydration), with substantial variation in the best predictor variables across given droughts. We conclude that when droughts occur, large dominant trees, drought-sensitive species, and individuals in wetter microhabitats are likely to be most strongly affected.

Introduction

Understanding how and why trees respond to drought is critical to predicting forest drought responses and climate change feedbacks. (1 paragraph on this- I have lots of content on this and will add later.)

[Understanding forest responses to drought requires increased functional understanding of the factors that confer individual-level vulnerability or resistance.] Forests are diverse in terms of tree sizes and functional traits, and it is known that trees varying in size and functional traits respond differently to drought (e.g., (Bennett et al., 2015); REFS). Therefore, in order to understand whole-forest response to drought, we need a functional understanding of how responses vary by tree size, microhabitat, and species. There are 3 fundamental questions that must be addressed:

First, what drives the observed tendency for large trees to suffer more during drought?

(Bennett et al., 2015) showed that in forests globally, large trees suffer greater growth reductions during drought. However, this analysis quantified tree size based on DBH, which has no direct mechanistic meaning. This study proposed two major mechanisms (besides insects) for the observed greater drought growth reductions of large trees: (1) inherently greater biophysical challenge of being tall; (2) greater exposure of the crowns of large trees. Counteracting these effects, (3) the larger root systems of larger trees may confer an advantage in terms of allowing greater access to water, but it appears that this effect is usually insufficient to offset the costs of height and/or crown exposure.

Second, how do species' traits—alone and in interaction with tree size—influence drought response? Analyzing drought responses on the species level does not fully explain mechanisms and is not feasible in diverse forests. The solution is a trait-based approach. Leaf hydraulic traits hold more promise than more commonly/traditionally-measured traits such as wood density and SLA (Medeiros et al. 2019).

Moreover, there may be an interaction between traits and tree size. It is possible that the pattern observed by (Bennett et al., 2015) could be caused by smaller trees being more drought resistant. Alternatively, larger trees may have more drought-resistant traits as adaptations to greater biophysical challenges.

Third, are responses similar or variable across individual drought years? Droughts are rarely explicitly defined in ecological studies (Slette et al., 2019), yet no two droughts are the same. This study addressed this by analyzing trees' resistance to drought within and across three defined drought periods.

Hypotheses

1. Why do larger trees suffer greater growth declines during drought?

1.0. Consistent with most forests globally (Bennett et al., 2015), larger-diameter trees have lower drought resistance. (Note that Bennett et al. 2015 identified only one study on tree growth responses to drought in the Eastern US temperate deciduous biome. We know little about how tree size shapes drought response in this biome.)

* P1.0-Drought resistance decreases with DBH at time of drought. (supported most of the time)

1.1. Drought resistance decreases with tree height.

* P1.1- Drought resistance decreases with height at time of drought, and height is a better predictor than diameter

1.2. Canopy trees have lower drought resistance because they are exposed to higher solar radiation, greater wind speeds, and lower humidity. Alternatively, the generally suppressed status of subcanopy trees may be insufficient to override the benefits of their buffered environment during drought. * P1.2a- Canopy position is a better predictor of resistance than height, with trees currently in a dominant canopy position having lowest resistance. (rejected) * P1.2b- After accounting for height, trees currently in a dominant canopy position have lowest resistance. (partially supported)

1.3. During drought, larger trees are at a relatively smaller disadvantage in drier microenvironments where rooting volume/depth is more important for reliable water access.

- P1.3- There is a negative interactive effect between tree height and topographic water index. (issue #45)

2. How do species' traits—alone and in interaction with tree size—influence drought response?

2.1. Commonly measured traits including wood density (REFS), leaf mass per area (Abrams, 1990) (Guerfel et al., 2009), and ring porosity (Elliot et al. 2015, Friedrichs et al. 2009) have been linked to drought responses and likely correlated with drought resistance in this forest. However, we hypothesize that leaf hydraulic traits such as leaf area shrinkage upon dessication and turgor loss point, which are emerging as potentially more informative traits but whose effect on drought resistance has never been tested (CONFIRM), will prove better predictors. * P2.1 - wood density correlates positively drought resistant * P2.2 - leaf mass area correlates positively to drought resistance * P2.3 - diffuse porous species are more sensitive than ring porous * P2.4 -leaf area shrinkage upon dessication (PLA) is negatively correlated with drought resistance (supported as one of the best predictors) * P2.5 - TLP correlates negatively with drought resistance (supported as one of the best predictors)

2.2. Traits vary with microenvironment, with more drought-resistant traits associated to taller trees (and drier topographic positions) (issue #43)

- * P2.2a- traits (all 5 above) correlate with tree height
- * (P2.2b- traits (all 5 above) correlate with TWI)

2.3. Size-dependent drought resistance is driven by—or alternatively, buffered by—functional traits (i.e., larger trees have more drought vulnerable traits). * P2.3 Inclusion of traits in the statistical model does not eliminate or significantly reduce effect of tree size (or TWI). That is, the effects of height and microhabitat will not be negated in the best model including size, microhabitat, and traits. (supported)

3. Did responses vary across droughts? 3.1 Overall community response is proportional to the severity of each drought.

* P3.1 - (How do you define severity? min PDSI? duration? it may be tricky to find the right metric, b

3.2. Predictor variables varied across droughts.

* P3.2 - There will be overall consistnecy in terms of the directions of responses to predictor variabl

Methods

Study site Research was conducted at the 25.6 ha ForestGEO (Global Earth Observatory) study plot at the Smithsonian Conservation Biology Institute (SCBI) in Virginia, USA (38°53'36.6"N, 78° 08'43.4"W) (Anderson-Teixeira et al., 2015a). SCBI is located in the central Appalachian Mountains at the northern edge of Shenandoah National Park. Elevations range from 273-338m above sea level (Gonzalez-Akre et al., 2016) with a topographic relief of 65m (Bourg et al., 2013). Dominant species include *Liriodendron tulipifera*, oaks (*Quercus* spp.), and hickories (*Carya* spp.).

Data collection and preparation The SCBI ForestGEO plot was censused in 2008, 2013, and 2018 following standard ForestGEO protocols, whereby all free-standing woody stems ≥ 1 cm diameter at breast height (DBH) were mapped, tagged, measured at DBH, and identified to species (Condit, 1998). From this census data, we used measurements of DBH from 2008 to calculate historical DBH (described below), along with tree location in the plot to determine the topographic wetness index. *I think that's it, really, in terms of data we're using coming from the censuses.*

We analyzed tree-ring data from the twelve species contributing most to woody aboveground net primary productivity (ANPP), which together comprised 97% of study plot ANPP between 2008 and 2013 (Helcoski et al., 2019). Cores were obtained in 2010-2011 or 2016-2017 from a breast height of 1.3m using a 5mm increment borer. In 2010-2011, cores were collected from randomly selected live trees were selected at random from each species, with at least 30 of those trees having a diameter at breast height (DBH) of at least 10cm (Bourg et al., 2013). In 2016-2017, cores were collected from all dead trees found in the annual mortality census (Gonzalez-Akre et al., 2016). Cores were sanded, measured, and cross-dated using standard procedures, as detailed in (Helcoski et al., 2019). The resulting chronologies have been published in association with Helcoski et al. (2019): (ITRDB). *is this a database?*

Height measurements ($n=\#$ trees) were taken by several researchers between 2012 to 2019, and are archived in a public GitHub repository. Measurement methods included manual (Stovall et al., 2018a, NEON), digital rangefinders (Anderson-Teixeira et al., 2015b), and automatic LiDAR (Stovall et al., 2018b). Rangefinders either used the tangent method (Impulse 200LR, TruPulse 360R) or the sine method (Nikon ForestryPro) for calculating heights. The associated errors for using either method were acknowledged (Larjavaara and Muller-Landau, 2013). Species-specific height allometries were developed (Table S# - **ADD THIS TABLE TO SI**). For species that didn't have enough height measurements, heights were calculated from equations derived from all species in the study.

For each tree, we combined tree-ring records and allometric equations of height and bark thickness to retroactively calculate DBH and estimate height for the years 1950-2009. Prior DBH was estimated using the following equation, using 2008 as the earliest year for having reliable DBH measurements:

$$diamYEAR = dbh2008 - 2 * (bark.depth2008) - 2 * \Sigma(ring.widthYEAR : ring.width2008) + 2 * (bark.depthYEAR)$$

Here, *ring.width* was measured from cores. Bark thickness was estimated from species-specific allometries based on the bark thickness data of (Anderson-Teixeira et al., 2015b). Specifically, we used linear regression equations on log-transformed data to relate bark thickness to DBH (Table S#- **create table to give these equations in SI**) and then used these to estimate bark thickness based on DBH.

Crown positions were recorded in the field during the growing season of 2018 following the crown position protocol from (Jennings et al., 1999), whereby positions were ranked as dominant, codominant, intermediate,

or suppressed. As there was no way to retroactively estimate crown position, we assumed that 2018 crown position was reflective of each tree’s position over the past 60 years. While some trees undoubtedly changed position, an analysis of crown position relative to height (Fig. XX) and height change since 1959 indicated that change was likely slow. **[work on this– provide details?]**

Topographic wetness index (TWI) was calculated using the (Metcalf et al., 2018) package in R.

Hydraulic traits were collected from SCBI and are summarized in Table 1. In August 2018, we collected leaf samples from three individuals of each species ... **(Nobby’s description of methods for the following)**

1. PLA 2. LMA 4. Wood density 5. TLP

Table 1. Species analyzed here, listed in descending order of ANPP_stem. n cores and DBH range represented, and species traits [*This replaces/combines the two remaining tables in this section. Suggested columns, with those to include only if they fit in parentheses: species, (stems ≥ 10 cm per ha in plot), (ANPP_stem), n cores, DBH range of cores, (n cores in each crown position) species means for each trait]

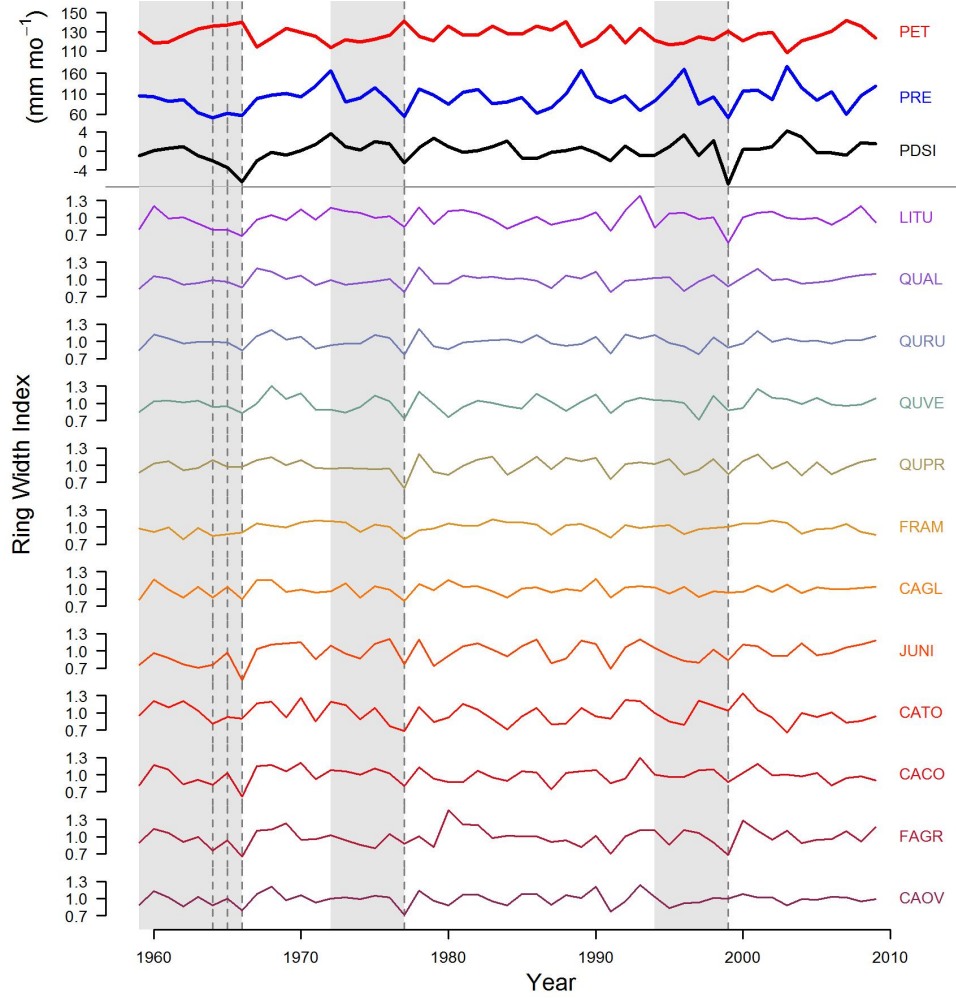
sp	n_cores	dominant	co-dominant	intermediate	suppressed	prior dead
caco	13	NA	2	5	5	1
cagl	31	1	8	16	5	1
caovl	23	4	5	12	2	NA
cato	13	NA	NA	6	2	5
fagr	80	NA	7	48	25	NA
fram	62	NA	17	19	14	12
juni	31	NA	21	8	NA	2
litu	98	9	29	25	30	5
qual	61	4	34	20	3	NA
qupr	59	1	26	20	12	NA
quru	69	6	36	23	2	2
quve	77	6	46	22	1	2

Trait	Unit	mean	min	max
Ring Porosity	ring, semi-ring, diffuse	NA	NA	NA
Percent Leaf Area	%	15.09	8.52	24.64
Leaf Mass Area	g/m ²	53.50	30.68	75.80
Wood density	g/cm ³	0.70	0.40	1.09
TLP	MPa	-2.36	-2.76	-1.92

Climate and drought years **[add description of climate data used in Fig. 1, NEON vertical profiles]**

To accurately understand climate sensitivity, this study used a specific definition of drought, which is not a common practice (Slette et al., 2019). We used the pointRes package (van der Maaten-Theunissen and van der Maaten, 2016) in R (version 3.5.3) to determine drought periods based on trees’ drought resistance, which is defined by (Lloret et al., 2011) as the ratio between the performance during and before the disturbance. Candidate drought years were defined if $>50\%$ of the cored trees experienced $<30\%$ growth in a year compared to the previous 5 years. These were then cross-validated with the regional Palmer Drought Severity Index (PDSI) values for each year, which yielded a set of three periods that were consistently shown as drought: 1964-1966, 1977, and 1999.

Figure 1. Time series of peak growing season (May-August) climate conditions and residual chronologies for each species. Droughts analyzed here are indicated by dashed lines, and shading indicates the pre-drought period used in calculations of the resistance metric. Figure modified from (Helcoski



et al., 2019).

Results

Once the data was collected, linear mixed models were run following the order of the hypotheses as seen in Figure ??? [individual_tested_traits]. Using the (van der Maaten-Theunissen and van der Maaten, 2016) package, we set up models with the resistance value as the response variable, and each prediction's variable as the independent variable. Variables' importance in predicting drought tolerance was calculated from mixed-effects models and the lowest AICc (Bates et al., 2019, Mazerolle and portions of code contributed by Dan Linden. (2019)). Null models were determined in order of the predictions. First, we analyzed the combined scenario to determine if "year" was significant. Upon establishing this, we tested height and DBH as size parameters. Although both were significant, height was kept due to its larger delta AICc compared with the null model. We then tested the remaining biophysical and hydraulic traits individually against a null model containing height and year. This yielded Figure ??? (cand_full). All variables with $\Delta AICc > 2$ were used as candidates for each scenario's best model (figure ??? (tested_traits_best))

Table 1: All variables tested for climate sensitivity against appropriate null models, in line with hypothesis predictions. Each variable was tested for each drought scenario excepting "year"

prediction	variable	variable_description	null_model	tested_model
1.1	year	drought.year	resist.value \sim (1 sp/tree)	resist.value \sim (1 sp/tree)+year
2.1	dbh.ln.cm	ln[DBH]	resist.value \sim year+(1 sp/tree)	resist.value \sim year+(1 sp/tree)+dbh.ln.cm
2.2	height.ln.m	ln[height]	resist.value \sim year+(1 sp/tree)	resist.value \sim year+(1 sp/tree)+height.ln.m
3.3	position_all	crown.position	resist.value \sim height.ln.m+year+(1 sp/tree)	resist.value \sim height.ln.m+year+(1 sp/tree)+position_all
3.4	TWI	topographic.wetness.index	resist.value \sim height.ln.m+year+(1 sp/tree)	resist.value \sim height.ln.m+year+(1 sp/tree)+TWI
4.1	rp	ring.porosity	resist.value \sim height.ln.m+year+(1 sp/tree)	resist.value \sim height.ln.m+year+(1 sp/tree)+rp
4.2	PLA_dry_percent	percent.leaf.area	resist.value \sim height.ln.m+year+(1 sp/tree)	resist.value \sim height.ln.m+year+(1 sp/tree)+PLA_dry_percent
4.3	LMA_g_per_m2	leaf.mass.area	resist.value \sim height.ln.m+year+(1 sp/tree)	resist.value \sim height.ln.m+year+(1 sp/tree)+LMA_g_per_m2
4.4	mean_TLP_Mpa	mean.turgor.loss.point	resist.value \sim height.ln.m+year+(1 sp/tree)	resist.value \sim height.ln.m+year+(1 sp/tree)+mean_TLP_Mpa
4.5	WD_g_per_cm3	wood.density	resist.value \sim height.ln.m+year+(1 sp/tree)	resist.value \sim height.ln.m+year+(1 sp/tree)+WD_g_per_cm3

Table 2: Candidate variables to be included in full model, chosen by $\text{dAICc} > 2$ when individually tested against a null model

	prediction	variable	variable_description	top_model
	1.1	year	drought.year	all
	2.2	height.ln.m	ln[height]	all
	2.2	height.ln.m	ln[height]	1966
	3.3	position_all	crown.position	1999
	3.4	TWI.ln	topographic.wetness.index	all
	3.4	TWI.ln	topographic.wetness.index	1977
	3.4	TWI.ln	topographic.wetness.index	1999
	4.1	rp	ring.porosity	1999
	4.2	PLA_dry_percent	percent.leaf.area	all
	4.2	PLA_dry_percent	percent.leaf.area	1966
	4.4	mean_TLP_Mpa	mean.turgor.loss.point	all

Table 3: Best full models for each drought scenario

best_model	r2	scenario
resist.value ~ year+height.ln.m+position_all+TWI+PLA_dry_percent+mean_TLP_Mpa+(1 sp/tree)	0.13	all droughts
resist.value ~ height.ln.m+rp+PLA_dry_percent+(1 sp)	0.24	1964-1966
resist.value ~ TWI+rp+mean_TLP_Mpa+(1 sp)	0.21	1977
resist.value ~ height.ln.m+position_all+TWI+rp+PLA_dry_percent+(1 sp)	0.25	1999

Discussion

1. paragraph summarizing main results—> primary conclusions When including only biophysical traits, trees’ resistance value (on a per-species basis) is explained best by crown position and height, with codominant trees being the most resistant to drought. This follows on work done by (Bennett et al., 2015) [and others?] which show that larger trees suffer more during drought, and confirms that this susceptibility can be seen in tree ring analyses. Adding in crown position with the leaf hydraulic traits yields a slightly worse predictive model for drought tolerance, with height remaining as the only significant biophysical variable.

We partially supported the hypothesis that crown exposure makes trees more vulnerable to drought. Co-dominant trees had the highest drought resistance. Dominant trees had lower resistance, likely because they are the most exposed. Other studies have found clear evidence of greater drought sensitivity in trees with exposed crowns (e.g., (Suarez et al., 2004); (Scharnweber et al., 2019)). At the same time, intermediate and suppressed trees had even lower resistance. This indicates that other mechanisms such as competition or rooting depth were important. (Also note that our study design was not ideal for testing the role of canopy position. Current canopy position is a conservative separator of canopy position: trees may currently be in more dominant positions than they were at the time, but backwards movement is unlikely. This would bias against finding a significant effect for H1.2. Height may be a more reliable predictor of past canopy position than is current canopy position, and explains a portion of variation in canopy position.)

Proximity to stream—either vertical (elev) or horizontal (distance)—did not increase drought resistance; rather, it tended to decrease resistance (H1.3a). This may be because individuals growing further from water are acclimatized to drier conditions. However, the increase in drought resistance with distance from stream was less for small than large trees (H1.3b), indicating a potential importance of root depth/volume in conferring drought resistance.

misc content to integrate From (Kannenberget al., 2019), species with diffuse porous wood anatomy (*Liriodendron*) are more sensitive to drought, whereas ring-porous are not as affected because they more

easily rebuild structures for hydraulic conductivity. This paper mentions it would be good to have this data with respect to latent affects from drought. ### Conclusion

words

Supplementary Information

SCBI ForestGEO Plot

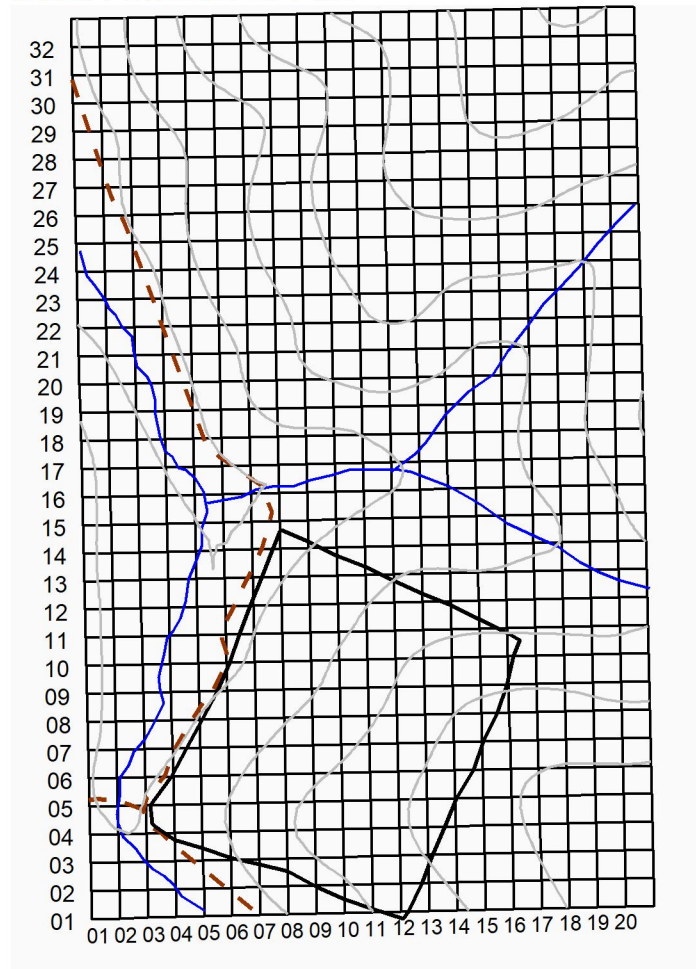


Figure 1: Map of ForestGEO plot

p50 and p80 We decided to include values of P50 and P80 in the leaf traits model, defined by (Anderegg et al., 2016) as the water potentials at which a species loses 50% and 88% [80% by proxy], respectively, of hydraulic conductivity. Values were calculated by (**insert new methods here??**), and were only available for six species (*C. glabra*, *L. tulipifera*, *Q. alba*, *Q. prinus*, *Q. rubra*, and *Q. velutina*). Because of this, the model runs were considered to be incomplete due to the exclusion of the other 8 species. Results revealed neither p50 nor p80 to be significant, thus for the full analysis we decided to drop the two traits in order to include all species in the full analysis.

(see Issue #32)

include TWI by trait graphs (2) here

Table 4: Species-specific height regression equations

Species	Equations	r.2
<i>Carya cordiformis</i>	$0.348+0.808*x$	0.879
<i>Carya glabra</i>	$0.681+0.704*x$	0.855
<i>Carya ovalis</i>	$0.621+0.722*x$	0.916
<i>Carya tomentosa</i>	$0.776+0.701*x$	0.894
<i>Fagus grandifolia</i>	$0.708+0.662*x$	0.857
<i>Liriodendron tulipifera</i>	$1.32+0.524*x$	0.761
<i>Quercus alba</i>	$1.14+0.548*x$	0.647
<i>Quercus prinus</i>	$0.44+0.751*x$	0.869
<i>Quercus rubra</i>	$1.17+0.533*x$	0.773
all	$0.879+0.634*x$	0.857

References

- Abrams, M. D. (1990). Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiology*, 7(1-2-3-4):227–238.
- Anderegg, W. R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A. F. A., Choat, B., and Jansen, S. (2016). Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences*, 113(18):5024–5029.
- Anderson-Teixeira, K. J., Davies, S. J., Bennett, A. C., Gonzalez-Akre, E. B., Muller-Landau, H. C., Wright, S. J., Salim, K. A., Zambrano, A. M. A., Alonso, A., Baltzer, J. L., Basset, Y., Bourg, N. A., Broadbent, E. N., Brockelman, W. Y., Bunyavejchewin, S., Burslem, D. F. R. P., Butt, N., Cao, M., Cardenas, D., Chuyong, G. B., Clay, K., Cordell, S., Dattaraja, H. S., Deng, X., Detto, M., Du, X., Duque, A., Erikson, D. L., Ewango, C. E. N., Fischer, G. A., Fletcher, C., Foster, R. B., Giardina, C. P., Gilbert, G. S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Hargrove, W. W., Hart, T. B., Hau, B. C. H., He, F., Hoffman, F. M., Howe, R. W., Hubbell, S. P., Inman-Narahari, F. M., Jansen, P. A., Jiang, M., Johnson, D. J., Kanzaki, M., Kassim, A. R., Kenfack, D., Kibet, S., Kinnaird, M. F., Korte, L., Kral, K., Kumar, J., Larson, A. J., Li, Y., Li, X., Liu, S., Lum, S. K. Y., Lutz, J. A., Ma, K., Maddalena, D. M., Makana, J.-R., Malhi, Y., Marthens, T., Serudin, R. M., McMahon, S. M., McShea, W. J., Memiaghe, H. R., Mi, X., Mizuno, T., Morecroft, M., Myers, J. A., Novotny, V., Oliveira, A. A. d., Ong, P. S., Orwig, D. A., Ostertag, R., Ouden, J. d., Parker, G. G., Phillips, R. P., Sack, L., Sainge, M. N., Sang, W., Sri-ngernyuang, K., Sukumar, R., Sun, I.-F., Sungpalee, W., Suresh, H. S., Tan, S., Thomas, S. C., Thomas, D. W., Thompson, J., Turner, B. L., Uriarte, M., Valencia, R., Vallejo, M. I., Vicentini, A., Vrška, T., Wang, X., Wang, X., Weiblen, G., Wolf, A., Xu, H., Yap, S., and Zimmerman, J. (2015a). CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology*, 21(2):528–549.
- Anderson-Teixeira, K. J., McGarvey, J. C., Muller-Landau, H. C., Park, J. Y., Gonzalez-Akre, E. B., Hermann, V., Bennett, A. C., So, C. V., Bourg, N. A., Thompson, J. R., McMahon, S. M., and McShea, W. J. (2015b). Size-related scaling of tree form and function in a mixed-age forest. *Functional Ecology*, 29(12):1587–1602.
- Bates, D., Maechler, M., Bolker, B., and Walker, S. (2019). *lme4: Linear Mixed-Effects Models using 'Eigen' and S4*. R package version 1.1-21.
- Bennett, A. C., McDowell, N. G., Allen, C. D., and Anderson-Teixeira, K. J. (2015). Larger trees suffer most during drought in forests worldwide. *Nature Plants*, 1(10):15139.
- Bourg, N. A., McShea, W. J., Thompson, J. R., McGarvey, J. C., and Shen, X. (2013). Initial census, woody seedling, seed rain, and stand structure data for the SCBI SIGEO Large Forest Dynamics Plot. *Ecology*, 94(9):2111–2112.

- Condit, R. (1998). *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots*. Springer Berlin Heidelberg, Berlin, Heidelberg.
- Gonzalez-Akre, E., Meakem, V., Eng, C.-Y., Tepley, A. J., Bourg, N. A., McShea, W., Davies, S. J., and Anderson-Teixeira, K. (2016). Patterns of tree mortality in a temperate deciduous forest derived from a large forest dynamics plot. *Ecosphere*, 7(12):e01595.
- Guerfel, M., Baccouri, O., Boujnah, D., Chaïbi, W., and Zarrouk, M. (2009). Impacts of water stress on gas exchange, water relations, chlorophyll content and leaf structure in the two main Tunisian olive (*Olea europaea* L.) cultivars. *Scientia Horticulturae*, 119(3):257–263.
- Helcoski, R., Tepley, A. J., Pederson, N., McGarvey, J. C., Meakem, V., Herrmann, V., Thompson, J. R., and Anderson-Teixeira, K. J. (2019). Growing season moisture drives interannual variation in woody productivity of a temperate deciduous forest. *New Phytologist*, 0(0).
- Jennings, S. B., Brown, N. D., and Sheil, D. (1999). Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry: An International Journal of Forest Research*, 72(1):59–74.
- Kannenberg, S. A., Novick, K. A., Alexander, M. R., Maxwell, J. T., Moore, D. J. P., Phillips, R. P., and Anderegg, W. R. L. (2019). Linking drought legacy effects across scales: From leaves to tree rings to ecosystems. *Global Change Biology*, 0(ja).
- Larjavaara, M. and Muller-Landau, H. C. (2013). Measuring tree height: a quantitative comparison of two common field methods in a moist tropical forest. *Methods in Ecology and Evolution*, 4(9):793–801.
- Lloret, F., Keeling, E. G., and Sala, A. (2011). Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, 120(12):1909–1920.
- Mazerolle, M. J. and portions of code contributed by Dan Linden. (2019). *AICcmodavg: Model Selection and Multimodel Inference Based on (Q)AIC(c)*. R package version 2.2-2.
- Metcalfe, P., Beven, K., and Freer, J. (2018). *dynatopmodel: Implementation of the Dynamic TOPMODEL Hydrological Model*. R package version 1.2.1.
- Scharnweber, T., Heinze, L., Cruz-García, R., van der Maaten-Theunissen, M., and Wilmking, M. (2019). Confessions of solitary oaks: We grow fast but we fear the drought. *Dendrochronologia*, 55:43–49.
- Slette, I. J., Post, A. K., Awad, M., Even, T., Punzalan, A., Williams, S., Smith, M. D., and Knapp, A. K. (2019). How ecologists define drought, and why we should do better. *Global Change Biology*, 0(0):1–8.
- Stovall, A. E. L., Anderson-Teixeira, K. J., and Shugart, H. H. (2018a). Assessing terrestrial laser scanning for developing non-destructive biomass allometry. *Forest Ecology and Management*, 427:217–229.
- Stovall, A. E. L., Anderson-Teixeira, K. J., and Shugart, H. H. (2018b). Terrestrial LiDAR-derived non-destructive woody biomass estimates for 10 hardwood species in Virginia. *Data in Brief*, 19:1560–1569.
- Suarez, M. L., Ghermandi, L., and Kitzberger, T. (2004). Factors predisposing episodic drought-induced tree mortality in *Nothofagus*—site, climatic sensitivity and growth trends. *Journal of Ecology*, 92(6):954–966.
- van der Maaten-Theunissen, M. and van der Maaten, E. (2016). *pointRes: Analyzing Pointer Years and Components of Resilience*. R package version 1.1.3.